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丛枝菌根真菌对百喜草的生理特性的影响*

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摘要：采用盆栽法研究了丛枝菌根（AM）真菌摩西球囊霉（*Glomus mosseae*）对水分胁迫条件下百喜草（*Paspalum notatum*）生长、渗透调节及抗氧化酶的影响。结果表明：接种 AM 真菌显著提高了百喜草的株高、地上部与根部鲜重、地上部 P、K、Mn 及根部 P、Ca、Mn 含量，明显降低了地上部 Zn 及根部 Fe、B、Cu 水平；随着干旱程度的加深，接种株的地上部相对含水量及叶绿素含量相对稳定且均显著高于未接种株，接种株地上部相对电导率、MDA 含量均显著低于未接种株，接种株的地上部 POD 活性与脯氨酸含量均显著增加且均显著高于未接种株，AM 侵染对 SOD 活性的影响较小。可见，接种 AM 真菌 *Glomus mosseae* 提高了植株体内保护酶活性（如 POD）及渗透调节能力（如脯氨酸、P、K、Ca 等渗透调节物含量的增加），从而显著增强了百喜草的抗旱性。

关键词：丛枝菌根真菌；百喜草；抗氧化物质；渗透调节；水分胁迫

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Effects of Arbuscular Mycorrhizal Fungi on Physiological Character of Bahia Grass (*Paspalum notatum*, Poaceae)

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Abstract: The effects of arbuscular mycorrhizal (AM) fungus, *Glomus mosseae*, on growth, osmotic adjustment and antioxidant enzymes of bahia grass (*Paspalum notatum*) were studied in potted plants under water stress conditions. AM colonization significantly enhanced the plant height, root and shoot fresh weight, Phosphorus (P), potasium (K), manganese (Mn) contents in shoots, P, calcium (Ca), Mn contents in roots, whereas obviously decreased zinc (Zn) content in shoots, iron (Fe), boron (B), copper (Cu) contents in roots. During water stress, the relative water and chlorophyll contents were relatively stable and signifciantly higher in AM than in non-AM plants, AM inoculation notabley decreased the shoot relative conductivity and malondialdehyde (MDA) content, markedly increased shoot peroxidase (POD) activity and proline content, while AM infection did not affect the dismutase (SOD) activity of shoots. Our results suggested that AM colonization improved the protective enzyme activity (such as POD) and osmotic adjustment originating from proline P, K, Ca, resulting in the enhancement of drought tolerance.

Key words: Arbuscular mycorrhizal fungi; Bahia grass; Antioxidant; Osmotic adjustment; Water stress

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Drought stress limits production of crop plants, particularly in arid and semi-arid areas (Kramer and Boyer, 1997). Arbuscular mycorrhizal (AM) fungal symbiosis is a mutualistic association between AM fungi and the roots of terrestrial plants, the ancient fungi can colonize approximately 80% of the Earth's land plant species, it's well documented that adaptive AM fungi inoculation can enhance the drought tolerance of host plant such as citrus (Wu *et al.*, 2005, 2006; Wu and Xia, 2006), and caragana korshinskii (He *et al.*, 2009a). In general, AM plants show higher stomatal conductance, transpiration rates, hydraulic conductivity and leaf water potential under water stress conditions, indicating that AM plants maintained more normal water relations (Auge, 2004). However, the mechanisms by which AM fungi have enhanced the water relations of host plants are still unclear. Potential mechanisms mainly include enhanced absorption of water by external hyphae (Ruiz-Lozano and Azcon, 1995), stomatal regulation through hormonal signals (Goicoechea *et al.*, 1997), indirect effect of improved phosphorus (Fitter, 1988), and a greater osmotic adjustment in AM plants (Ruiz-Lozano, 2003).

Sod culture in orchard not only can effectively avoid water and soil erosion, but also can enhance organic matter, mineral content in soil (Li *et al.*, 2007), hence, it is thought to be an important planting technology in modern ecotype orchard. Presently, bahia grass (*Paspalum notatum* Flugge) is widly applied to sod culture in orchard of China (Li *et al.*, 2005, 2007), which can increase fruit tree (such as citrus plant) root colonization by arbuscular mycorrhizae, and improve nutritional level and fruit quality (Zeng *et al.*, 2004; Li and Ying, 2005; Ren *et al.*, 2009). Whereas, information about the effects of AM fungi on growth, osmotic adjustment and reactive oxygen metabolism of common grass of sod culture in orchard like baiha grass is scarce. The purpose of this study is to, evaluate the effects of *Glomus mosseae* on growth, osmotic active solutes and antioxidant enzymes of bahia grass under water stress conditions, the result will play a theoretical and basic role taking practical steps for production in the area.

Materials and methods

Experimental materials and growth conditions

Seeds of bahia grass were surface-sterilized with 70% alcohol for 5 min and germinated on wet filter paper in Petri dishes in darkness at 25℃. Seven days after germination, seedlings were transplanted to a plastic pot containing 3.0 kg of an autoclaved growth substrate (0.11 MPa, 121℃, 2 h) of yellow soil and quartz sand (9 : 1, v/v), the characteristic of which were: pH 6.1, 1.2% organic matter, available P 11.05 $mg \cdot g^{-1}$, available K 39.28 $mg \cdot g^{-1}$, available Ca 394.07 $mg \cdot g^{-1}$, available Mg 11.33 $mg \cdot g^{-1}$, available Zn 0.47 $mg \cdot g^{-1}$, available Cu 0.09 $mg \cdot g^{-1}$. The soil was collected from the Experimental Sample Garden, Anhui Normal University (Wuhu, China), The experimental pots were placed in a greenhouse under natural light conditions without any temperature control from April to June. The inoculated and non-inoculated bahia grass were irrigated once every 2 day. The average day/night temperature was 30/25℃ during water stress, and average air relative humidity was 80%. AM and non-AM plants were not fertilized during the entire experiment.

Mycorrhizal fungus inocula

Mycorrhizal fungus inocula, consisting of spores, soil, hyphae and infected root fragments from a stock culture of *Glomus mosseae* (No. BGC HUN01A), were provided by Bank of Glomales in China, Institute of Plant Nutrition and Resources, Beijing Academy of Agriculture and Forestry Sciences. The inoculated dosage was 20 g of inocula per pot containing approximately 1488 spores. Mycorrhizal inocula were placed 5 cm below baiha grass roots at the time of transplanting. Non-AM treatments received the same mass of autoclaved growth substrate.

Experimental design

The present experiment was a completely randomized 2×2 factorial design, with two mycorrhizal treatments, AM fungus and non-AM fungus, and four water treatments, cut off water supply for 0 day, 4 days, 8 days, and water supply restored for 4 days. Water stress treatment began after 75 days (June 15, 2009) of acclimation in greenhouse conditions. Each of the eight treatments was replicated four times, leading to a total of 32 pots.

Plant growth and mycorrhizal colonization measurement

At the time of water stress treatment began, A fraction of the plants were harvested and plant height, fresh weight of shoots and roots were recorded. The shoots and roots were separated and dried at 75℃ for 48 h. A fraction of fresh roots were carefully washed and cut into 1 cm root pieces to fix in formalin-acetic acid-alcohol solutions, these roots were cleaned with 10% (w/v) KOH and stained with 0.05% (w/v) trypan blue in lactophenol (Phillips and Hayman, 1970), and microscopically observed for root colonization. The AM infected percentage was counted by the following formula: AM infected percentage (%) = 100 × root length infected/root length observed.

Inorganic ions analyses

Hundred milligrams of dry shoots or roots were used to extract inorganic ions with 20 mL 1 mol · L^{-1} hydrochloric acid at 40℃ for 2 h, and then filtered through a piece of filter paper. Phosphorus (P), potasium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), zinc (Zn), boron (B) and copper (Cu) concentrations in the dried shoots and roots were determined by inductively coupled plasma optical emission spectrometry (ICP-OES, Iris-Advantage type, USA).

Relative water content, chlorophyll content and relative conductivity determination

The equation relative water content (RWC) (%) = 100 × (FW-DW)/(SW-DW) was used for RWC calculation, where FW stood for fresh weight, DW for dry weight, and SW for saturated weight, SW was determined after floating the shoot on distilled water for 24 h at the room temperature. Shoot chlorophll content and relative conductivity were assayed according to Li (2003). The extraction was made from 50 mg-fresh sample in 25 mL acetone (80%) in the dark at the room temperature and was measured at 646 and 663 nm with a UV/VIS spectrophotometer. Relative conductivity was determined by conductivity meter (DDS-307).

Determination of SOD and POD acitivities, MDA and proline contents

Another fraction of the plants were harvested at the water treatment time (0 d, 4 d, 8 d and 12 d), Samples were quick freezed by liquid nitrogen, and stored in refrigerator for superoxide dismutase (SOD), peroxidase (POD) activities, malondialdehyde (MDA) and proline contents analysis. Extracts for determination of SOD, POD were prepared from half a gram of fresh shoot tissue homogenized in 5 mL of 0.1 mol · L^{-1} phosphate buffer (pH 7.8) containing 0.1 mmol · L^{-1} EDTA, 1 mmol · L^{-1} ASC, 1 mmol · L^{-1} 1,4-dithiothreitol and 2% (w/v) polyvinylpyrrolidone and centrifuged at 4 200 *g* for 10 min, with the resulting supernatant used for assays. All steps of the extraction procedure were carried out at 4℃. SOD activity was measured using the method of Giannopolitis and Ries (1977). One unit of SOD was defined as the amount of enzyme that inhibited 50% nitro blue tetrazolium by light, and SOD activity was expressed as SOD units per mg of protein. POD activity was determined using the method of Chance and Maehly (1955). Five hundred mg of fresh shoots were homogenized in 5 mL of 5% (w/v) trichloroacetic acid and centrifuged at 3 000 *g* for 10 min. MDA of extracts was determined by the thiobarbituric acid reaction as described by Sudhakar *et al.* (2001).

For proline determination, fresh samples were extracted with 3% sulfosalicyclic acid, placed in a boiling water bath for 10min and filtered through filter paper. Two milliliter of extract was added to 6 mL assay media containing 2 mL ninhydrin solution and 2 mL acetic acid and incubated for 30 min at

100℃ and then cooled. The colored product formed was extracted with 4 mL toluene by shaking and the absorbance of resultant organic layer was measured at 520 nm (Troll and Lindsley, 1955).

Statistical analysis

The experimental data were subjected to analysis of variance (ANOVA) using the Statistical Analysis System (SAS 8.1) software. For comparison of the means, the Duncan's multiples range test was employed.

Results and analysis

No mycorrhizal colonization was observed in the roots of non-AM plants. The roots of plants inoculated with *Glomus mosseae* were infected. AM plants had significant plant height, shoot and root fresh weight than corresponding non-AM plants (Table 1).

Phosphorus, K contents in shoots, P, Ca contents in roots were higher in AM plants than those in non-AM plants, and the P, K levels were notably higher in shoots than in roots of both AM and non-AM plants, whereas, AM colonization did not affect the Mg contents in shoots and roots (Table 2).

The contents of Mn in shoots and roots of AM plants were significantly higher than those in non-AM plants, while shoot Zn content, root Fe, B, Cu contents were substantially lower compared with corresponding non-AM plants, Fe contents were higher in roots than in shoots of AM and non-AM plants (Table 3).

As the water stress progresses, shoot relative water content was decreasing degressively in non-AM plants, whereas, changed slightly in AM plants. During water stress, relative water contents were significantly higher in AM than in non-AM plants (Fig. 1: A).

Chlorophyll contents of shoots were decreasing degressively in non-AM and AM plants with the increase of drought degree, and shoot chlorophyll contents were higher in AM than in non-AM plants at the stage of water stress (Fig. 1: B).

Table 1 Root and shoot characteristics of AM and non-AM *Paspalum notatum* plants

AM fungus status	Root colonization (%)	Plant height (cm)	Leaf fresh weight (g·plant^{-1})	Root fresh weight (g·plant^{-1})
non-AM fungus	0.00a	23.33±3.06a	0.25±0.02a	0.11±0.02a
AM fungus	33.87±5.16b	41.67±2.89b	0.49±0.04b	0.45±0.04b

Data are Means±SD. the same letters within a column indicate no significant differences at $P<0.05$. The same is in the following tables

Table 2 Phosphorus, K, Ca and Mg concentrations in shoots and roots of AM and non-AM *Paspalum notatum* plants

AM fungus status	P (mg·g^{-1} DW)		K (mg·g^{-1} DW)		Ca (mg·g^{-1} DW)		Mg (mg·g^{-1} DW)	
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
non-AM fungus	1.18±0.19a	0.52±0.10a	23.16±0.11a	12.57±0.83a	8.70±0.15a	5.58±1.14a	2.47±0.38a	2.44±0.44a
AM fungus	1.95±0.01b	0.83±0.02b	30.99±4.34b	13.47±2.13a	10.16±1.71a	9.00±0.66b	2.65±0.17a	3.06±0.25a

Table 3 Zinc, Fe, B, Cu and Mn concentrations in shoots and roots of AM and non-AM *Paspalum notatum* plants

AM fungus status	Zn (mg·kg^{-1} DW)		Fe (mg·kg^{-1} DW)		B (mg·kg^{-1} DW)		Cu (mg·kg^{-1} DW)		Mn (mg·kg^{-1} DW)	
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
non-AM fungus	27.47 ±4.18a	30.35 ±3.34a	85.55 ±12.82a	420.89 ±94.63a	22.8 ±0.58a	25.4 ±2.42a	21.68 ±2.03a	31.38 ±6.28a	17.53 ±2.50a	24.68 ±3.81a
AM fungus	16.95 ±2.19b	27.91 ±6.08a	76.78 ±6.81a	304.27 ±32.77b	15.07 ±3.94a	12.76 ±7.59b	19.93 ±2.16a	20.62 ±2.08b	46.70 ±3.00b	58.75 ±6.24b

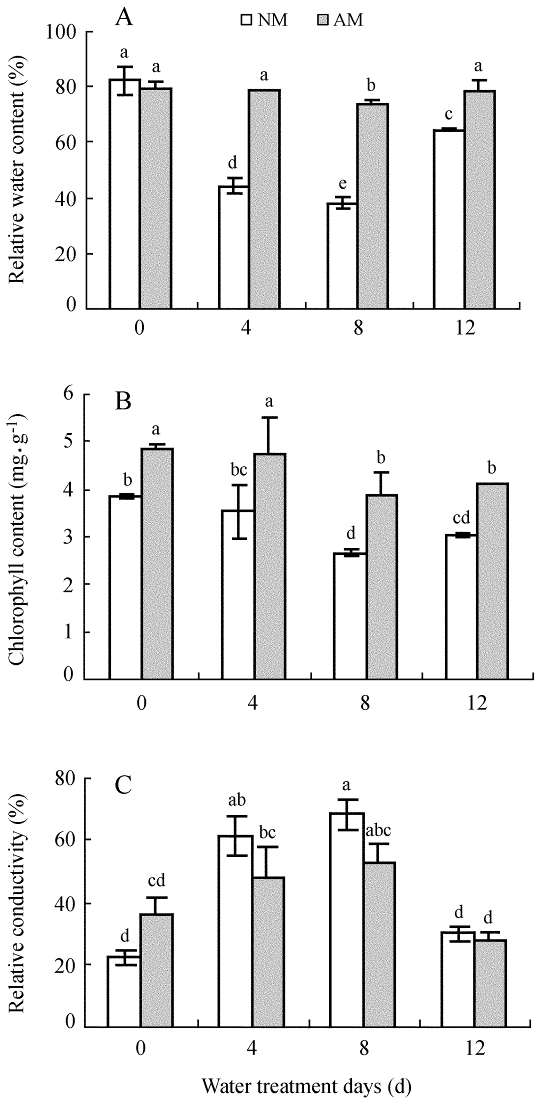

Fig. 1　Relative water content (A), chlorophyll content (B), and relative conductivity (C) of shoots in AM and non-AM *Paspalum notatum* plants subjected to water stress *Note*: NM, non-AM plants; AM, AM plants. The same is in the following figure

Relative conductivity of shoots in non-AM plants markedly increased at the time of water stress for 4 days and 8 days, but no significant difference was observed on shoot relative conductivity in AM plants during water stress compared with corresponding water stress before (Fig. 1: C).

Shoot SOD activities in non-AM and AM plants, shoot POD activities in AM plants were increasing progressively as the water stress progresses (Fig. 2: A, B), but no significant change was found on shoot POD activities in non-AM plants, and during water stress, shoot POD activities were conspicuously higher in AM than in non-AM plants (Fig. 2: B). MDA contents of shoots were significantly higher in non-AM than in AM plants during water stress (Fig. 2: C). No significant change was observed on proline in shoots from non-AM plants during the time of water stress, whereas, the shoot proline contents obviously increased in AM plants, and were significantly higher than those in non-AM plants (Fig. 2: D).

Discussion

We observed the positive effects of AM fungus, *Glomus mosseae*, on the growth, the biomass and P, K, Ca contents of bahia grass (Table 1, 2), which indicated that AM colonization enhanced P uptake by roots and its upward transportation, leading to the plants' increasing growth and the other elements such as K, Ca absorption by roots. Similar results have been reported for other plant species (Wu and Zou, 2007; Kapoor *et al.*, 2008; Miransari *et al.*, 2009a; He *et al.*, 2009b). Phophorus is generally believed to be removing poorly in the soil, the grand hyphal net formed in the soil by AM can travel across P deficiency area around the root, which can enhance the contact with the soil and turn unavailable P around root into available P to roots, the improvement of P, K, Ca absorption by AM plants, and the direct uptake and transport of the extraradical hypha outside the roots are all likely to increase the P, K, Ca levels in plant, which is consistent with the findings that the field grass cultivation can effectively increase the contents of P, K in citrus leaves (Li and Yi, 2005; Ren *et al.*, 2009), and we suggested that the grass such as bahia grass in orchard have highly developed root system and be easily infected by AM fungi, which is beneficial to the soil mineral elements, and thus promote P, K, Ca uptake by roots. Additionally, AM fungi inoculation also significantly increased Mn contents in shoots and roots of bahia grass, but notably reduced Zn in

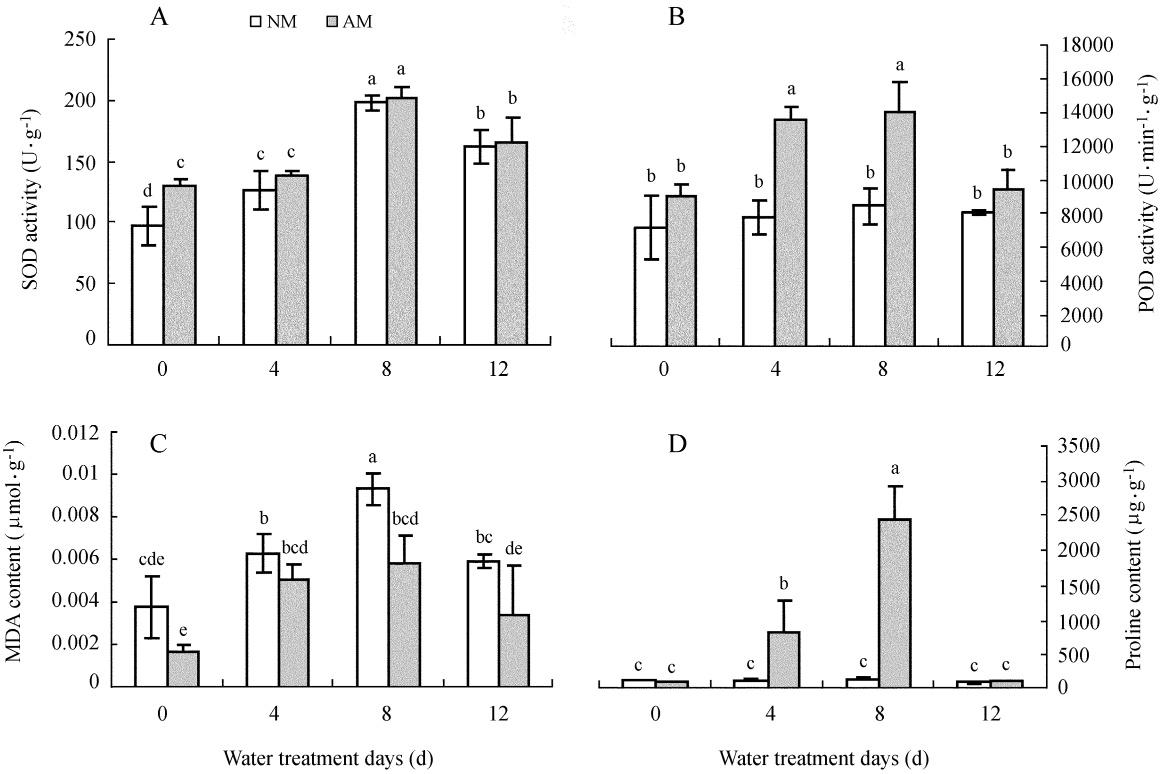

Fig. 2 Superoxide dismutase (SOD) (A) and peroxidase (POD) (B) activities, and malondialdehyde (MDA) (C) and proline (D) contents of shoots in AM and non-AM *Paspalum notatum* plants subjected to water stress

shoots and Fe, B, Cu in roots (Table 3), which is not all in accordance with previous investigation on trifoliate orange (Wu and Zou, 2007), corn (Miransari *et al.*, 2009a) and wheat (Miransari *et al.*, 2009b). Generally, AM colonization has an influence on the number of reducing bacteria by the mineral elements such as Mn in the rhizosphere soil as well as the reducing power of the rhizosphere. However, there existed differences for different hosts infected by different AM fungi varieties, namely, AM symbiosis and its host has different selectivity and adaptability, for example, AM fungi inoculation promoted iron uptake by trifoliate orange roots, while this whole process may be affected by the soil pH value (Wang and Xia, 2009), additionally, soil moisture conditions (Song *et al.*, 2008), P level (He *et al.*, 2009a), or nitrogen level (He *et al.*, 2009b) all affected soil nutrient uptake by the roots infected by AM. Moreover, there is a mutual beneficial and antagonistic relationship among mineral elements in the soil and plant. Thus, the differences of research findings mentioned above should not only be due to the species and characters of AM fungi and their hosts, but also attribute to the interaction between the mineral elements in the soil and plants.

Water content in plant tissue can reflect cell water status, and chlorophyll is the most important and effective pigment in photosynthesis, which can demonstrate the assimilation ability in plant. This research showed that during water stress, AM plants have a stable relative water and chlorophyll contents, which were higher than those in non-AM plants (Fig. 1), this result showed that AM fungi inoculation can release the influence of water stress on water metabolism and photosynthesis in shoots, and improve the physiological status in order to strengthen the anti-drought stress ability.

Water stress can induce ROS, as a result of lipid peroxidation and production of MDA (Lacan and Baccou, 1998). Our study proved that there was less MDA and relatively conductivity levels in AM bahia grass shoots, enhancing drought tolerance of AM plants. When plants are subjected to water stress, activities of a number of antioxidant enzymes are enhanced in order to elimilate ROS (Ruiz-Lozano, 2003). Wu *et al.* (2006) reported that activities of SOD, POD and CAT were usually higher in AM than in non-AM roots under well-watered and water stress conditions. In our results, under water stress conditions, SOD activities increased in AM and non-AM plants, while POD activity and proline content increased significantly in shoots from AM plants and were higher than those in non-AM plants (Fig. 2). It is well known that the important function of SOD is to remove superoxide free radicals so as not to generate H_2O_2, which is then elimilated by POD and CAT. As a result, AM inoculation can remove the accumulation of reactive oxygen caused for the water stress by improving SOD and POD activities, and adjust cell osmotic potential to protect the activities of enzyme systems by promoting the accumulation of proline as well as P, K, Ca, with the aim of reducing the damage caused by membrane lipid peroxidation, which in return enhance the drought tolerance of bahia grass.

In short, *G. mosseae*-inoculation had a positve effect on growth, osmotic adjustment, and reactive oxygen metabolism of bahia grass, increasing the concentrations of proline, P, K, and POD in shoots, and decreasing the shoot relative conductivity and MDA content. The result suggested that the benefit of AM colonization under water stress conditions was due to the enhancement of osmotic adjustment and higher antioxidant enzymes, and AM fungi inoculation would be a new way relieasing the problems for drought existed in sod culture in orchard.

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